Prosopis glandulosa and the nitrogen balance of rangelands: extent and occurrence of nodulation

H.B. Johnson and H.S. Mayeux, Jr.

Grassland, Soil and Water Research Laboratory, U.S. Department of Agriculture, Agricultural Research Service, Temple, TX 76502, USA

Summary. We report the recovery of root nodules from *P. glandulosa* var. *glandulosa* in the eastern portion of its range, where the species reaches its greatest vegetational development. Single cores 4.7 cm in diameter and up to 250 cm deep yielded from 0 to over 250 nodules. Nodules were found at all depths below 10 cm, with the highest concentration often around 100 cm. Detailed studies of three trees revealed relatively small volume densities of about 0.02 nodules cm^{-3}, high surface area densities of 2–4 nodules cm^{-2}, and high nodule biomass of 8–23 g m^{-2}, when compared to cultivated legumes. Nodules are small, weakly attached to roots that are seldom over 0.5 mm in diameter, and not easily observed under field conditions. No nodules were recovered from cores from the more arid western portion of *P. glandulosa*'s range, although seedlings nodulated readily in these soils in the glasshouse as well as in most unamended soils from throughout mesquite's geographical range. Local differences in nodulating potential of soils included a negative association with mesquite canopies and a positive association with depth. These results suggest a significant role for biological fixation in the nitrogen regime and vegetation dynamics of *Prosopis*-dominated ecosystems.

Key words: *Prosopis glandulosa* – Mesquite – Nodulation – Nitrogen fixation – Vegetation change

---

Prosopis glandulosa var. *glandulosa* (Leguminoseae, Mimosoideae), honey mesquite, is a conspicuous component and common dominant woody plant in natural vegetation on approximately 45 million ha of rangelands of the southwestern United States and northern Mexico. It has been introduced and become naturalized in other parts of the world. Its North American distribution extends from western Louisiana (longitude 94°) on the east through New Mexico (longitude 108°) on the west and from southern Kansas (latitude 37°) on the north into Tamaulipas, Mexico (latitude 25°) on the south (Fig. 1). The average annual rainfall across this range varies from less than 20 cm in the west to over 100 cm in the east. Western honey mesquite, *P. glandulosa* var. *torreyana*, and velvet mesquite, *P. velutina*, overlap honey mesquite's distribution in the western portion of its range.

Prosopis is one of the most important genera associated with the dramatic increase of woody plants on former grasslands of the American Southwest and southern Great Plains, a phenomenon first recognized around the turn of the century (Bentley 1898; Cook 1908; Wooten 1908). Since then, spectacular examples of these changes in vegetation have been documented (Branson 1985) and are still in process. Causes of these changes are most often attributed to the disturbance associated with selective grazing of grasses by domestic livestock, spread of seed in livestock dung, and managers' efforts to eliminate or suppress range fires, as well as changes in climate or short-term weather patterns such as droughts. However, it is becoming apparent that replacement of open grasslands by shrubs and larger woody species and rapid thickening of existing stands of woody plants proceeds even when these factors are eliminated. This suggests that other factors and processes are involved (Johnson 1985).

An hypothesis for an indirect contributing factor is that the available nitrogen reserves of rangeland soils have been reduced by intensive and prolonged grazing (Woodmansee 1978) and that low nitrogen status limits the successful development or competitive ability of some species, especially grasses, more than others (Gilbert 1982). Available soil nitrogen is widely regarded as the factor most limiting plant productivity, next to water, on rangelands. Thus it is not unreasonable to assume that nitrogen fixing plants should have a competitive advantage in a nitrogen stressed environment. Nevertheless, little research has been conducted on the extent of biological nitrogen fixation in the nitrogen regimes of rangelands. The significance of nitrogen fixation in vegetation dynamics has been considered most often in
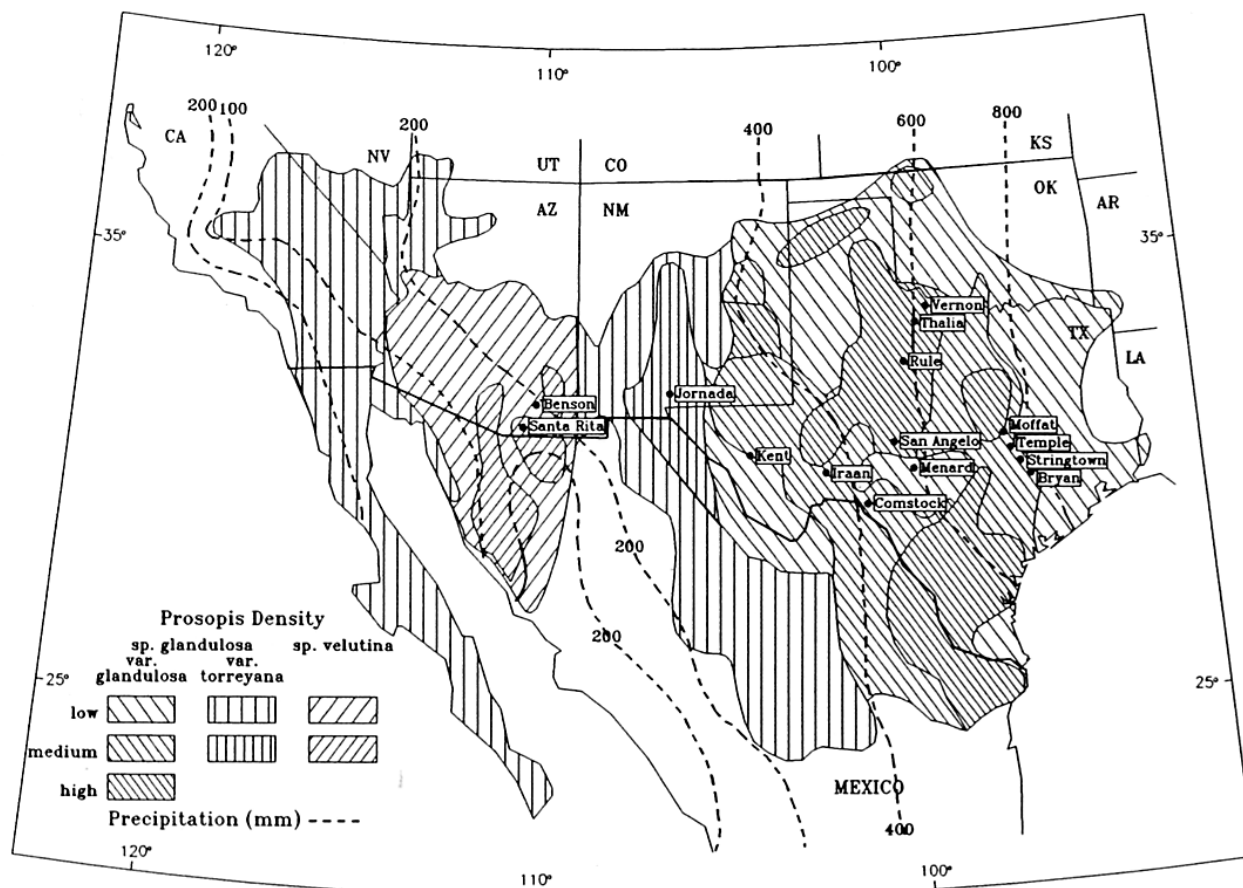
Offprint requests to: H.B. Johnson

Fig. 1. Geographic distribution and density of *Prosopis glandulosa* var. *glandulosa*, *P. glandulosa* var. *torreyana*, and *P. velutina* in the United States and Mexico. Place names indicate the collection sites for soil cores for nodule analysis and soil samples for determining soil nodulating potential. All sites were well drained uplands. Low density = mesquite ground surface cover less than 10%. In the arid West, it represents widely scattered individual plants or widely spaced clusters as occur in occasional sinks and dune systems or as narrow bands of stringers along drainage ways, mostly as phreatophytes. Toward the more humid East, it represents areas where *Prosopis* persists along fence rows and field boundaries over large areas that are under cultivation or where it occurs as a minor component of multiple-species woody vegetation. Medium density = *Prosopis* ground surface cover between 10 and 20%. *Prosopis* is a dominant species in the vegetation of well-drained uplands. High density = *Prosopis* ground cover greater than 20%. *Prosopis* vegetation is the major vegetation development in the landscape. Dashed lines indicate mean annual precipitation in mm. States are abbreviated. Map data sources: Leopold 1951; Parker and Martin 1952; Johnston 1963; Hastings et al. 1972; Vines 1976; Martin and Hutchings 1980; Benson and Darrow 1981; Garrison and McDaniel 1982; and Soil Conservation Service 1987

studies of plant succession where changes in soil nitrogen are considered a causal force in the replacement of one species assemblage by another (Crocker and Major 1955; Vitousek et al. 1987; Archer et al. 1988).

A dictum of symbiotic nitrogen fixation is that soil rhizobia must be present to induce root nodules on a host plant as sites for the nitrogen fixing process (Postgate 1982). The occurrence of nodules on roots is used extensively as a probable indicator of atmospheric nitrogen fixation by members of the legume family (Lin and Ng 1977). An exhaustive survey of observations of the presence or absence of nodulation was compiled for the entire family by Allen and Allen (1981). In the case of the genus *Prosopis*, reports from the laboratory and the field do not agree. Screenings of species for nodulating ability under controlled conditions routinely yielded positive results for the genus (e.g. Felker and Clark 1980), but efforts to recover nodules from the roots of mesquite trees in the field have been much less successful (Martin 1948; Bailey 1976).

Failures to find nodules have led to questioning whether mesquite acts as a nitrogen fixer in the field (Allred 1949; Barth and Klemmedson 1982), which in turn relates directly to the hypothesis that biological nitrogen fixation acts as a driving force in the vegetation change that is now taking place on rangelands. Indeed, consideration of nitrogen fixation in relation to what has been termed "the mesquite problem" is conspicuously absent from the proceedings of symposia, conferences, and general appraisals of the subject (Parker and Martin 1952; Glendening and Paulsen 1955; Fisher et al. 1959; Scifres et al. 1973; Simpson 1977; Soltes

1977; Whitson and Scifres 1980; Parker 1982). Only De-Loach (1986) addresses the question, and he concludes that too little information is available to resolve the issue.

This question is addressed here in a review of the history of nodule observations for the genus, which serves as preface to a report of our investigations. Our objectives were to determine whether nodulation of honey mesquite roots occurs in the field, especially under non-phreatic conditions on well-drained uplands that prevail over most of the species' distribution (Fig. 1), assess the nodulating capacity of selected soils from honey mesquite's geographic distribution, and consider the implications of these results and those in the literature on the nitrogen regime and changes in vegetation of rangelands.

Nodulation of mesquite seedlings was observed as long ago as 1931 by Lechtova-Trnk for what is probably *P. laevigata* but was reported then as *P. dulcis* (Allen and Allen 1981; Burkart 1976). Wilson (1939) reported on nodulation relationships of over 200 species in 70 legume genera, including a taxon identified as *P. juliflora*, which then embraced honey mesquite, *P. glandulosa* var. *glandulosa* as defined today (Johnston 1962). Honey mesquite seedlings nodulated with rhizobial strains isolated from twelve different legume species. A significant paper by Khudairi (1957) not only reports the presence of root nodules on *P. stephaniana* (*P. fracta*, Burkart 1976) seedlings in pots but also observations of nodules on roots in the field. Allen and Allen (1981) report the nodulation of three species in the glasshouse through personal communication; *P. vidaliana* (now *P. juliflora*) with Lenard in 1938, *P. chilensis* with Paul in 1951, and *P. juliflora* var. *glandulosa* (now *P. glandulosa* var. *glandulosa*) with Burton in 1971. Gupta and Balara (1972) found nodules on *P. juliflora* seedlings in the glasshouse. Grobbelaar and Clark (1974) listed *P. chilensis* among the species that nodulated in their laboratory screening of a large number of legumes. Basak and Goyal (1975) found that *P. cineraria* and *P. juliflora* seedlings were nodulated by indigenous rhizobia in India.

Bailey (1976) found that seedlings nodulated readily in the greenhouse in north Texas soils from cultivated fields as well as from sites supporting mesquite. However, he failed to find nodules on honey mesquite roots at five sites sampled to a depth of 1 m. Nonetheless, Bailey found it difficult to believe that root nodules did not occur on mesquites growing in their natural environment and suggested that he sampled at the wrong time of year. He hypothesized that nodules are only present seasonally, perhaps for just a few months of the year.

Bailey's demonstration of ready nodulation of mesquite seedlings in the laboratory encouraged additional work on the question. Eskew and Ting (1978) measured nitrogen fixation by nodules of *P. glandulosa* var. *torreyana* seedlings, using acetylene reduction in the glasshouse. Felker and Clark (1980) nodulated 12 species of *Prosopis* in the glasshouse with the rhizobial strain obtained from mesquite by Eskew and Ting. Virginia et al. (1984) and Baird et al. (1985) reported variations in mes-

quite nodule morphology and the nitrogen fixing efficiency of different rhizobia associated with greenhouse-grown western honey mesquite nodules.

The parallel search for nodules in the field continued to be disappointing and did not meet the expectations that came from the easy and abundant nodulation observed in pot culture. In all the early reports of nodulation of mesquite, only Khudairi (1957), working in Iraq, clearly states that nodules were found on roots of a *Prosopis* (*P. stephaniana*) in the field as well as on seedlings in the laboratory. Subsequent workers largely ignored, doubted, or were unaware of Khudairi's study. From the 1940's to the present, the consensus view of nitrogen fixation by honey mesquite largely followed the lead of Martin (1948) who failed to find nodules on *P. glandulosa* in the field or on *P. velutina* and *P. pubescens* in a nursery. For instance, Felker and Clark (1982) write that there are no published reports of *Prosopis* nodulation in the field and cite two personal communications of recent field observations of nodulation. In the first, Cornejo observed nodules on *P. glandulosa* var. *torreyana* in an atypically moist coastal environment in Mexico. In the second, Virginia and Jarrell recovered nodules from the same taxon along a stream in southern California. The latter were recovered from a depth of 2 m (Virginia and Jarrell 1983). Nodulated seedlings of *P. velutina* were later observed in a field nursery in Tucson, Arizona (personal communication with Tom Johnsen 1984).

As recently as 1985, Shoushtari and Pepper mistakenly state, but understandably so, that *Prosopis* nodulation has not been observed in a natural field situation. More recently, Jenkins et al. (1987) accurately observed that researchers have recovered very few nodules from mesquite roots in the field, but reported that they found nodules on western honey mesquite seedlings and on older plants at their arid study site in the Sonoran Desert.

Other evidence suggests that mesquites in the field are indeed involved in the acquisition of considerable amounts of atmospheric nitrogen. A strong indication for biological nitrogen fixation was obtained from measurements of the natural abundance of ^{15}N in tissue from *P. glandulosa* var. *torreyana* in areas where it functions as a phreatophyte in the Sonoran Desert (Shearer et al. 1983). The $^{15}N/^{14}N$ ratio of leaf tissue was more like that of the air than that of non-leguminous reference plants growing with the mesquites. We have also acquired ^{15}N natural abundance data that indicates dinitrogen fixation by non-phreatophytic *P. glandulosa* var. *glandulosa* (Johnson and Mayeux 1988), as have Lajtha and Schlesinger (1986) for non-phreatophytic *P. glandulosa* var. *torreyana*. Further, comparatively large amounts of nitrogen have been observed to accumulate in the soils under the canopies of mesquite (Tiedeman and Klemmedson 1973; Virginia and Jarrell 1983; Klemmedson and Tiedeman 1986). Such evidence for nitrogen fixation led Felker and Clark (1982) to carry out nodulation experiments in 3 m long soil columns with an imposed water table near the bottom. They concluded that mesquite nodulates at the moist fringe above the water

table. This concept is supported by observations that where mesquite functions as a phreatophyte, rhizobial densities increase with soil depth and are particularly dense near the ground water interface (Virginia et al. 1986).

It is clear from the literature that most authors consider all *Prosopis* to be phreatophytes (Nilse et al. 1981). This is not the case for *P. glandulosa* var. *glandulosa*, which sometimes behaves as a phreatophyte in the western portion of its range but grows mostly as a nonphreatophyte. Honey mesquite is particularly abundant on well-drained uplands in the central third of its range (Fig. 1). Overall, it covers a much larger proportion of the ground surface in the landscapes where it occurs than does western honey mesquite.

Honey mesquite appears to be a typical species of the genus *Prosopis*. An understanding of its effects on nitrogen regimes should be helpful in characterizing nitrogen relationships of its close relatives in other parts of the world. A score of *Prosopis spp.* are major components of the world's vegetation in semiarid to arid regions. *P. alba*, *P. chilensis*, *P. nigra*, and *P. pallida* are identified by Burkart (1976) as being particularly important and valuable trees of arid lands in South America and other places where they have been introduced. Two others, *P. ruscifolia* and *P. velutina*, are economically important rangeland weeds, the former in Argentina and the latter in the United States.

Methods and materials

We examined soil cores extracted from directly beneath *Prosopis* canopies of a total of 10 locations (Fig. 1). Seven of these, all in Texas, were dominated by honey mesquite. One, the Jornada Experimental Range in southern New Mexico, supported western

honey mesquite. The two most western sites, in Arizona, supported velvet mesquite.

Core length varied from 65 to 300 cm, depending upon soil and site characteristics. A single core was taken beneath most trees, but 11 to 18 cores were extracted from beneath each of three trees at the Temple, Texas location. Soil cores were collected at Temple at irregular intervals for about 1 year beginning in May 1985. Cores were taken at increasing distances from the base of the trees on selected dates.

Two different coring devices were used. A portable, manual corer consisted of steel tubes with an inside diameter of 45 mm, each 1 to 3 m long. A heavy steel casing was welded to one end of each tube so that tubes could be driven into the soil and a jack could be attached for extracting the tube from the soil. These were used in remote locations. A tractor-mounted, hydraulically operated soil coring system was employed at the Temple site. Coring tubes were 42 mm in diameter, 120 cm long and could be joined in extensions.

Cores were divided into 10 or 20 cm depth increments. All plant material was removed from each soil increment by placing it in 4 L of water and adding 30 ml concentrated HCl to dissolve carbonates. The water was periodically and gently stirred to encourage plant materials to float free. Roots and nodules were removed by sieving with 0.3- to 2-mm screens and were carefully inspected under magnification. The number and type of nodules were recorded. Nodules from selected cores were oven-dried and weighed.

The presence of root nodules establishes a plant's capacity to produce them, but failure to find nodules does not establish the lack of such ability. A lack of nodules may be due to the absence of the appropriate rhizobial strain(s) or inappropriate environmental conditions for the symbiotic association to become established, as well as inherent deficiencies in the genetics of the host plant (Meiger 1982). Consequently, the nodulation potential of 16 soils from 11 locations within honey mesquite's geographic range was determined in the glasshouse. Five of these sites were those sampled for presence of nodules. Nodulation potential is defined by the percentage of seedlings which nodulated and the average number of nodules that develop per seedlings for each soil. Most soil samples were taken from the surface horizon directly underneath mesquite trees but soils were also taken from interspaces between mes-

Table 1. Inventory of root nodules found in soil cores taken from underneath *Prosopis glandulosa* var. *glandulosa* canopies at five locations in Texas

Location	Tree no.	Soil texture	Number of cores	Nodules per core	Depths (cm)		
					Core depth	First nodule	Greatest density
Temple	1	silty clay	18	28	90–180	5	50–100
Temple	2	silty clay	11	42	130–190	5	20– 70
Temple	3	silty clay	17	61	130–220	5	20–140
Moffat	1	clay	1	27	65	10	20– 65
Moffat	2	sandy loam	2	20	110	10	10– 50
Moffat	3	sandy loam	1	7	110	10	10– 50
Stringtown	1	clay	1	12	100	50	40– 60
Stringtown	2	clay	1	11	100	10	60– 80
Stringtown	3	clay	1	9	100	20	80–100
Stringtown	4	clay	1	16	100	10	40– 80
Stringtown	5	clay	1	16	100	20	40– 80
Stringtown	6	clay	1	26	100	10	20– 80
Stringtown	7	clay	1	3	100	80	80–100
Stringtown	8	clay	1	2	100	10	10– 40
Stringtown	9	clay	1	0	100	–	–
Stringtown	10	clay	1	7	100	20	40– 80
Bryan	1	clay loam	1	74	110	10	20– 80
Vernon	1	sandy clay	1	37	180	30	90–150
Vernon	2	sandy clay	2	28	170	90	90–170

Table 2. Average number of nodules on *Prosopis glandulosa* var. *glandulosa* seedlings and percentage of seedlings with nodules when germinated in soils collected from several locations. The order of collection sites is from east to west

Location	Dominant vegetation	Soil texture	Seedling age (weeks)	Mean no. nodules per plant	Seedlings nodulated (%)
Temple TX 1	*Juniperus*	clay	8	11	100
Temple TX 1	fallow	clay	8	13	100
Temple TX 2	*Prosopis*	sandy loam	8	9	100
Temple TX 2	*Prosopis*	sandy loam	8	11	100
Thalia TX	*Ulmus*	sand	16	0	0
Rule TX	*Prosopis*	sandy loam	16	14	100
Menard TX	*Quercus*	loam	8	6	100
Menard TX	*Prosopis*	loam	8	0	0
San Angelo TX	grass	loam	8	11	100
Comstock TX	*Prosopis*	loam	8	5	100
Iraan TX	*Prosopis*	sandy loam	8	12	100
Kent TX	grass	sandy loam	8	2	80
Kent TX	*Prosopis*	sandy loam	8	1	30
Jornada NM	*Prosopis*	sandy loam	8	0.2	10
Jornada NM	grass	sandy loam	8	5	100
Benson AZ	*Prosopis*	sandy loam	8	3	80

Table 3. Average number of nodules on *Prosopis glandulosa* var. *glandulosa* seedlings and percentage of seedlings with nodules when germinated in soils collected from underneath *Prosopis* canopies or the interspace between canopies at three locations

Location	Nodules per plant		Percent plants nodulated	
	Mesquite	Interspace	Mesquite	Interspace
Menard TX	0	6.3	0	100
Kent Tx 1	0.4	2.1	25	80
Kent Tx 2	0.4	0.4	20	30
Jornada NM 1	0.2	5.8	10	100
Jornada NM 2	1.3	5.3	90	100

quite trees at five locations. At four sites, soils were excavated by depth increments to as much as 5 m for testing nodulation potential in the vertical dimensions of the soil profile.

Surface-sterilized honey mesquite seeds were planted in these soils in cone-shaped containers 4 cm in diameter and 20 cm long with a volume of approximately 200 cm^3. Ten repetitions of each soil or depth increment were prepared. The containers were placed in racks in the greenhouse and the soil was kept moist with deionized water during germination and growth. The seedlings were allowed to develop for 8–16 weeks, when root systems were washed free of soil and observed under magnification for the presence and number of nodules.

Results and discussion

Geographic distribution of nodules and nodulation potential of soils

We found numerous nodules on the roots of 19 honey mesquite trees at 5 locations in the eastern part of its distribution, in Texas (Fig. 1): near Temple, Moffat, Stringtown, Bryan and Vernon (Table 1). These findings are contrary to previous reports attesting to the scarcity or lack of nodules on mesquite trees in the field in the United States. However, in agreement with the literature, we failed to find nodules in our systematic sampling of soil cores from San Angelo and Iraan in western Texas, even though we observed nodules at the San Angelo site during earlier excavations of mesquite roots. We also failed to find nodules in cores obtained in January and September from under *P. glandulosa* var. *torreyana* from the Jornada Experimental Range in southern New Mexico and *P. velutina* from the two locations sampled in Arizona, near Benson and the Santa Rita Experimental Range (Fig. 1).

The lack of nodules in cores obtained in west Texas, New Mexico, and Arizona appears paradoxical since other evidence indicates that the mesquite from these areas should be fixing nitrogen. We have unpublished data on natural abundance patterns of ^{15}N, which indicate nitrogen fixation, and positive results from soil nodulation potential tests from these areas. Results of nodulation tests for soils from San Angelo, Iraan, Jornada Experimental Range, and Benson show that honey mesquite seedlings grown in soils from these sites nodulated just as well as those grown in soils from the areas where nodules were found in the field (Table 2). These data indicate that soils from throughout the study area contain rhizobia appropriate for inducing nodulation (also Bailey 1976). Mesquite seedlings failed to nodulate in only two to the sixteen soils tested. One was a blow sand from an *Ulmus* wind shelter belt near Thalia in north Texas and the other a dark loam surface soil from under a mesquite tree near Menard in central Texas.

The failure of mesquite seedlings to nodulate in the soil from under a mesquite canopy at the Menard site is of special interest because honey mesquite seedlings nodulated readily in a second soil sample from under a nearby *Quercus virginiana* (Table 2). This pattern of reduced nodulation in surface soils from under mesquite canopies relative to soils from the interspaces between mesquite trees was duplicated in soils from all five locations where the sampling procedure permitted such comparisons (Table 3). A similar change in nodulation potential was found in the vertical dimension. A pattern of increasing nodulation potential with depth was found for the soils from four of the sites (Table 4).

It is evident that the nodulating potential of soils can vary markedly on a local scale. The negative relationship between soil nodulation potential and the presence of mesquite was unexpected but may be partly explained in terms of mineral nitrogen accumulation. High soil nitrate is a well known nodulation inhibitor (Gibson and Harper 1985) and high nitrogen and nitrate levels

Table 4. Average number of nodules on *Prosopis glandulosa* var. *glandulosa* seedlings germinated in soil collected from underneath *Prosopis* canopies at various depth increments. Dashes indicate that no sample was obtained from that site at the depth increment shown

Depth increment (cm)	Nodules per seedling			
	San Angelo TX	Iraan TX	Jornada NM	Benson AZ
0– 15	3.0	11.8	0.2	–
0– 50	–	25.4	1.3	–
20– 50	–	–	–	2.8
25– 40	3.4	–	–	–
40– 50	11.0	–	–	–
50–100	–	–	6.5	–
100–125	–	25.9	–	–
100–150	–	–	5.9	–
100–200	–	–	–	4.0
150–200	–	–	15.6	–
300	–	–	–	3.7
500	–	–	–	5.3

Fig. 2. Nodule forms, all taken from a single *Prosopis glandulosa* var. *glandulosa* tree at Temple, Texas. From left to right and starting at the top, the nodule forms are globose, elongate, branched, and fan-shaped. Note the narrow nodule-root connections. The fan-shaped nodule at lower right is conspicuously flattened and attached to a ribbon-like root typical of those found in soil fracture planes at depths below 1 m. The grid increment is 1 cm

are reported for surface soils under mesquite canopies (Secor et al. 1983; Virginia and Jarrell 1983; Wright and Honea 1986). The increase in the nodulation potential with depth is the reverse of the expected nitrate distribution and in agreement with the rhizobial population distributions found by Virginia et al. (1986) and Jenkins et al. (1988).

Description of nodules

The morphology of mesquite nodules is highly variable (Fig. 2). Essentially all the basic shapes of nodules illustrated by Allen and Allen (1981) were found on roots of individual trees. These include globose, elongate, bifurcate, fan shaped (palmate), and coralloid. Of the many nodules observed on the three trees at Temple, approximately half were globose, a third were elongate, and the remainder were branched. Baird et al. (1985) found that nodule morphology was a function of the rhizobium population inducing nodule formation. Some of the differences in nodule shapes and sizes may be attributable to different species of rhizobia (slow and fast growing types) distributed at different levels in the soil profile as reported by Jenkins et al. (1989). Felker and Clark (1980) suggested that the different forms of mesquite nodules may represent different stages of maturity. Our observations also suggest that the nodular forms of honey mesquite are developmentally related. Those of simple globose structure may through further growth become elongated, branched or lobed. All nodules exhibited a brown leathery texture at maturity, regardless of morphological form. A capacity for perennial growth as noted by Allen and Allen (1981) was evident in the large older nodules where apical meristems appeared to initiate lobe extensions and new branches.

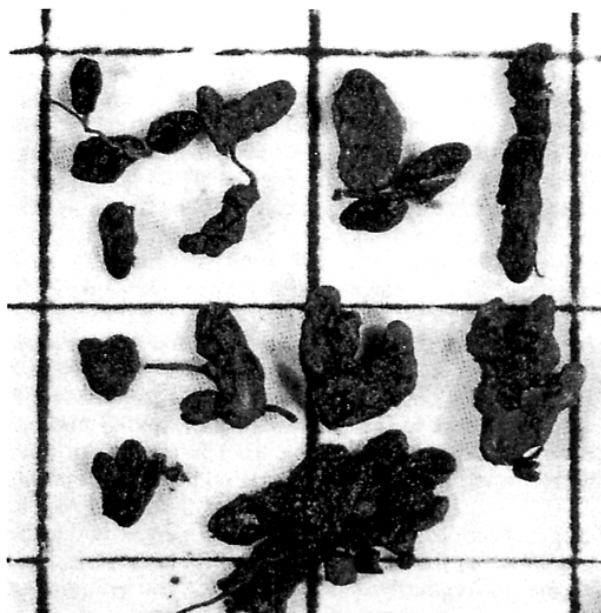Some unusual nodule forms were noted deep in the soil profile where soil bulk density and soil strength were high. Most notable were the compressed or flattened nodules associated with small ribbon-like roots growing along cleavage planes in the blocky structured, clayey subsoil. Other nodules from intermediate depths took the form of elongated cylinders appressed laterally to the small roots to which they were attached (Fig. 2).

Nodule length ranged from 0.2 to 12 mm with a mean of 1.7 mm. More than two thirds of the nodules were from 1 to 2 mm long. This nodule size appears small in comparison to those reported for crop plants and other woody plants, which commonly have nodules averaging greater than 3 mm in length (Boring and Swank 1984; Lim and Ng 1977). Mesquite nodules longer than 3 mm were usually elongated or branched.

Most nodules were detached from roots when recovered and some appeared fragmented. Roots with nodules attached were small and fragile and most measured about 0.5 mm in diameter. Nodules were almost never found on roots larger than 1 mm. Nodules were separated from these small roots with ease, a factor that may contribute to the difficulty of locating them in field excavations.

Spatial and temporal distribution of nodules

Nodules were found throughout the soil profiles at the sites examined in the eastern part of honey mesquite's range (Table 1). Eleven of the nineteen nodulated trees yielded nodules within 10 cm of the soil surface. Nodules

generally reached their highest densities at depths well below the surface. Nodules were also commonly recovered near the bottom of the deepest cores, around 3 m. The number of nodules per core at the five eastern sites varied from zero to over 250, with averages as shown in Table 1. The maximum core depths do not always represent the entire rooting profile of the soil. This is particularly true for the Stringtown site where the soil was arbitrarily sampled to a depth of 1 m. The number of nodules recorded per core would undoubtedly have been greater if cores had been longer; the number of nodules per core should therefore be regarded as a minimum when interpreted on the basis of land surface area.

Depths where nodule concentrations were greatest were not consistent among trees, probably reflecting differences in local soil properties and the spatial unevenness of root development (Fig. 3). The number of nodules recovered from cores along radial transects at points 0.3, 0.9, and 1.5 m from the base of the three trees at Temple show that nodules are well dispersed under the tree canopy in the horizontal plane (Table 5). Thus nodules are not regularly distributed in the soil volume but occur in patches scattered in both the vertical and horizontal planes. The diffuse pattern of occurrence contrasts with the assumptions commonly made in nodule studies of crop plants, that nodules are produced primarily in the top 15 to 20 cm of soil with a concentration around the taproot (Weil and Ohlrogge 1975; Grubinger et al. 1982; Weiser et al. 1985).

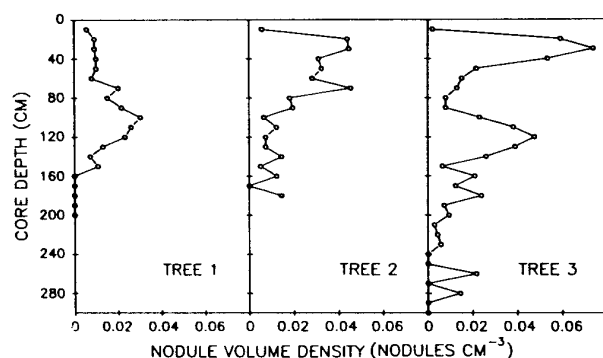The highly diffuse distribution of mesquite nodules

may be characteristic of other woody legumes and be directly related to the difficulty of locating nodules on some species in the field. Researchers working with species of *Leucaena* are generally unable to find nodules on plants more than a year old (Halliday and Somasegaran 1983). Hogberg (1986) states that up to 3 days were required to find nodules on woody legumes in the savannas of Tanzania. This suggests a dispersed distribution involving comparatively large volumes of soil. However, the concentration of nodules of *Robinia pseudoacacia* trees (Boring and Swank 1984) and *Alnus* species (Akkermans and Dijk 1976; Sharma and Ambasht 1986) near the soil surface indicates that diffuse distributions are not necessarily characteristic of woody plants.

Although limited, the year long sampling at Temple provides some information about nodule phenology. Nodules were recovered from all cores from under the Temple trees regardless of the month of year (January through December). Most nodules at the time of recovery were dark brown with a leathery texture. Actively growing nodules, commonly characterized by a pink coloration, were observed only in cores extracted from September through December. Vernon, the only other site sampled within this time frame (September) was also the only other site from which actively growing nodules were recovered.

Nodule density and biomass

Insight into the pattern of nodulation on mesquite roots is gained by consideration of nodule density and biomass on the basis of both soil volume and ground surface area. Nodule distribution expressed as volume density averaged across cores differed with depth among the three trees studied in detail (Fig. 3). The average volumetric density of nodules of whole cores from under mesquite canopies at Temple ranged from 0.010 to 0.017 nodules cm^{-3}. The ground surface density or areal density ranged from 2 to 4.4 nodules cm^{-2} (Table 6). Volume density was lower and areal density was higher in honey mesquite than in the bean, *Phaseolus vulgaris*; volume and areal density was calculated to be 0.051 nodules cm^{-3} and 0.76 nodules cm^{-2} (Sparrow and Ham 1983) and 0.034 nodules cm^{-3} and 0.346 nodules cm^{-2} (Weiser et al. 1985), respectively. Honey mesquite nodule densities differ from those of *Glycine max* (Weil and Ohlrogge 1975) in a similar manner. These differences

Fig. 3. Nodule volume density (nodules cm^{-3}) at 10 cm depth increments for three *Prosopis glandulosa* var. *glandulosa* trees sampled at Temple, Texas. Plotted values are averaged across 11 to 18 cores per tree and several sampling dates

Table 5. Average number of nodules per core for soil cores distributed radially around three *Prosopis glandulosa* var. *glandulosa* trees at Temple, Texas. Number of cores appears in parentheses

Tree no.	Distance from base of tree (m)		
	0.3	0.9	1.5
1	39 (6)	27 (5)	32 (5)
2	62 (5)	33 (2)	21 (5)
3	76 (5)	31 (3)	27 (5)

Table 6. Estimates of nodule volume density, areal density and mean dry nodule biomass of three mature *Prosopis glandulosa* var. *glandulosa* trees at Temple, Texas. Biomass extrapolations are based on weight per nodule relationships of representative cores and applied to the average number of nodules per core (Table 1)

Tree no.	Volume density (nodules cm^{-3})	Areal density (nodules cm^{-2})	Nodule weight (mg)	Weight density (g m^{-2})
1	0.010	2.03	0.43	8.67
2	0.017	3.04	0.515	15.66
3	0.015	4.42	0.59	26.12

between mesquite and the cultivated herbaceous legumes are due to a weak association of mesquite nodules with the tap root (greater areal dispersion) and distribution to far greater soil depths.

The oven-dry weight of honey mesquite nodules averaged about 0.5 mg (Table 6). Even though the size and volume density of mesquite nodules were low, the large number of nodules results in a relatively high nodule dry biomass, ranging from 8.7 to 26.1 g m^{-2}. These values are considerably larger than those reported for the woody plants (*Robinia pseudoacacia*, 3.5 g m^{-2} (Boring and Swank 1984) and *Cytisus scoparius*, 2.2 g m^{-2} (Wheeler et al. 1987), and approximate the range of values calculated for bean and soybean, 2 to 23 g m^{-2} (Weber 1966; Hunt et al. 1985; Weiser et al. 1985).

Nodulation and nitrogen fixation

Three possible explanations are suggested for our failure to find nodules in the soil cores from west Texas, New Mexico, and Arizona where soil nodulation potentials indicate the presence of appropriate rhizobia and ^{15}N natural abundance patterns indicate the likelihood of nitrogen fixation. First, nodules may have been produced but decomposed too rapidly to detect. All soils lacking nodules are of a type (sandy loams) that are characteristically well aerated and have high organic matter decomposition rates. Environmental conditions favorable to nodule development are sporadic in these arid areas. Second, nodule volume density may have been too low for nodules to be detected by the coring method. The small size and low nodule volume density characteristic of honey mesquite in central Texas may be even lower in more arid regions and more samples and more careful scrutiny may be required to detect them. Also, a progressive reduction in nodule volume density with time should be expected as nitrogen accumulates in the soil profile as evidenced by the systematic patterns in the nodulation potential of local soils associated with mesquite (Tables 3 and 4). Third, nodule predation was suggested by very conspicuous amounts of insect frass and body parts found in association with the mesquite roots. The existence of obligate nodule feeding insects is well documented (Rockwood 1951; Foote 1985; Quinn and Hower 1986).

The presence of nodules is deemed essential for nitrogen fixation, but the reverse is not necessarily true. Some agronomic legumes produce nodules that are ineffective in fixing atmospheric nitrogen (Lim and Burton 1982). A significant proportion of ineffective nodules are unlikely in the case of a highly successful species of natural plant communities such as *Prosopis glandulosa* var. *glandulosa*. The high energy cost of nodule production would serve as a detriment to the host plant's competitive ability without the compensating benefits of nitrogen fixation.

Nitrogen fixation rates can be estimated if we assume that the nodules on our field-grown honey mesquites are effective. Effective nodules on other legumes fix from 0.3 to 20 g N yr^{-1} g^{-1} of nodules (Weber 1966; Pate

1976; Boring and Swank 1982; Hunt et al. 1985). If we adopt a conservative nitrogen fixation rate of 1 g N yr^{-1} g^{-1} of nodules and use the nodule weights from Table 6, the calculated nitrogen fixation rates of non-phreatophytic honey mesquite at Temple range from 9 to 30 g N yr^{-1} m^{-2} of canopy cover, or 45 to 150 kg N ha^{-1} yr^{-1} at 50% canopy cover. These rates compare favorably with the 40 kg ha^{-1} yr^{-1} calculated for phreatophytic mesquite in California with about 30% cover (Rundel et al. 1982). When these projected rates are viewed in terms of the millions of hectares of honey mesquite with high canopy coverage (Fig. 1), it becomes clear that honey mesquite must be a significant contributor to the nitrogen budget of range ecosystems in the southwestern United States and Mexico and that the genus *Prosopis* is likely to play an important role on a global scale.

References

Akkermans ADL, Dijk C van (1976) The formation and nitrogen fixing activity of the root nodules of *Alnus glutinosa* under field conditions. In: Nutman PS (ed) Symbiotic nitrogen fixation. Cambridge University Press, London, pp 511–520

Allen ON, Allen EK (1981) The leguminosae. A source book of characteristics, uses and nodulation. University of Wisconsin Press, Madison, Wisconsin

Allred BW (1949) Distribution and control of several woody plants in Texas and Oklahoma. J Range Manage 2:17–29

Archer S, Scifres CJ, Bassham CR, Maggio R (1988) Autogenic succession in subtropical savanna: conversion of grassland to thornland. Ecol Monogr 58:111–127

Bailey AW (1976) Nitrogen fixation in honey mesquite seedlings. J Range Manage 29:479–481

Baird LM, Virginia RA, Webster BD (1985) Development of root nodules in a woody legume, *Prosopis glandulosa* Torr. Bot Gaz 146:39–43

Barth RC, Klemmedson JO (1982) Amount and distribution of dry matter, nitrogen, and organic carbon in soil-plant systems of mesquite and palo verde. J Range Manage 35:412–418

Basak MK, Goyal SK (1975) Studies on tree legumes: nodulation pattern and characterization of the symbiont. Ann Arid Zone 14:367–370

Benson L, Darrow RA (1981) Trees and shrubs of the southwest deserts. (3rd edition) University of Arizona, Tucson

Bentley HL (1898) Cattle ranges in the Southwest. A history of the exhaustion of the past uses and suggestions for its restoration. United States Department of Agriculture Farmer Bull 72

Boring LR, Swank WT (1984) Symbiotic nitrogen fixation in regenerating black locust (*Robinia pseudoacacia* L.). For Sci 30:528–537

Branson FA (1985) Vegetation changes on western rangelands. Range Monog 2, Soc Range Manage, Denver, Colorado

Burkart A (1976) A monograph of the genus *Prosopis* (Leguminosae subfam. mimosoideae). J Arnold Arboretum 57:217–249, 450–525

Cook OC (1908) Change of vegetation on the south Texas prairies. United States Department of Agriculture, Bureau of Plant Industries Circ No 14

Crocker RL, Major J (1955) Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J Ecol 43:427–448

DeLoach CJ (1986) Conflicts of interest over beneficial and undesirable aspects of mesquite (*Prosopis* spp) in the United States as related to biological control. In: Delfosse ES (ed), Proc.

VI International Symposium on Biological Control of Weeds, Vancouver, Canada. Minister of Supply and Services, Canada. pp 301–340

Eskew DL, Ting IP (1978) Nitrogen fixation by legumes and blue-green algal-lichen crusts in a Colorado desert environment. Am J Bot 65:850–856

Felker P, Clark PR (1980) Nitrogen fixation (acetylene reduction) and cross inoculation in 12 Prosopis (mesquite) species. Plant and Soil 57:177–186

Felker P, Clark PR (1982) Position of mesquite (Prosopis spp) nodulation and nitrogen fixation (acetylene reduction) in 3-m long phraetophytically simulated soil columns. Plant and Soil 64:297–305

Fisher CE, Meadors CH, Behrens R, Robinson ED, Marion PT, Morton HL (1959) Control of mesquite on grazing lands. Texas Agricultural Experiment Station Bull 935

Foote BA (1985) Biology of Rivellia pallida (Diptera; Platystomatidae), a consumer of the nitrogen-fixing root nodules of Amphicarpa bracteata (Leguminoseae). J Kansas Entomol Soc 58:27–35

Garrison GL, McDaniel KC (1982) New Mexico brush inventory. New Mexico Department of Agriculture Special Report No. 1

Gibson AH, Harper JE (1985) Nitrate effect on nodulation of soybean by Bradyrhizobium japonicum. Crop Science 25:497–501

Gilbert LE (1982) An ecosystem perspective on the role of woody vegetation, especially mesquite, in the Tamualipan biotic region of South Texas. Proc Symp Tamualipan Biotic Province, Corpus Christi, Texas

Glendening GE, Paulsen HA (1955) Reproduction and establishment of velvet mesquite as related to invasion of semidesert grasslands. United States Department of Agriculture Tech Bull 1125. p 50

Grobbelaar N, Clark B (1974) A qualitative study of the nodulating ability of legume species; list 4. Agroplantae 6:59–64

Grubinger V, Zobel R, Vendeland J, Cortes P (1982) Nodule distribution on roots of field-grown soybeans in subsurface horizons. Crop Science 22:153–155

Gupta RK, Balara GS (1972) Comparative studies on the germination, growth and seedling biomass of two promising exotics in Rajasthan Desert. Ind For 98:280–285

Halliday J, Somasegaran P (1983) Nodulation, nitrogen fixation and Rhizobium strain affinities in the genus Leucaena. In: Leucaena research in the Pacific region, Proceedings of a workshop held in Singapore, November 1982. International Development Research Centre, Ottawa, Canada

Hastings JR, Turner RM, Warren DK (1972) An atlas of some plants distributions in the Sonoran Desert. Univ of Ariz Tech Rpt no 21

Hogberg P (1986) Nitrogen-fixation and nutrient relations in savanna woodland trees (Tanzania). J Appl Ecol 23:675–688

Hunt PG, Matheny TA, Wollum II AG (1985) Rhizobium japonicum nodular occupancy, nitrogen accumulation, and yield for determinate soybean under conservation and conventional tillage. Agronomy J 77:579–584

Jenkins MA, Virginia RA, Jarrell WA (1987) Rhizobial ecology of the woody legume mesquite (Prosopis glandulosa) in the Sonoran Desert. Appl Environm Microbiol 53:36–40

Jenkins MB, Virginia RA, Jarrell WM (1988) Depth distribution and seasonal population fluctuations of mesquite – nodulating rhizobia in warm desert ecosystems. Soil Sci Soc Am J 52:1644–1650

Jenkins MB, Virginia RA, Jarrell WM (1989) Ecology of fast growing and slow growing mesquite nodulating rhizobia in Chihuahuan and Sonoran Desert ecosystems. Soil Sci Soc Am J 53:543–549

Johnson HB (1985) Consequences of species introductions and removals on ecosystem function – implications for applied ecology. In: Delfosse ES (ed), proc. VI International Symposium on Biological Control of Weeds, Vancouver, Canada. Minister of Supply and Services Canada. pp 27–56

Johnson HB, Mayeux HS (1988) Mesquite nodulation and nitrogen fixation on rangelands. Proc 41st Annual Meeting, Soc Range Manage. Abstract 296.

Johnston MC (1962) The North American mesquites Prosopis sect. Algarobia (Leguminosae). Brittonia 14:72–90

Johnston MC (1963) Past and present grasslands of southern Texas and northeastern Mexico. Ecology 44:456–466

Klemmedson JO, Tiedeman AR (1986) Long term effects of mesquite removal on soil characteristics: II. nutrient availability. Soil Sci Soc Am 50:476–480

Khudairi AK (1957) Root-nodule bacteria of Prosopis stephaniana. Science 125:399

Lajtha K, Schlesinger WH (1986) Plant response to variations in nitrogen availability in a desert shrubland community. Biogeochemistry 2:29–37

Leopold AS (1951) Mexico vegetation map. University of California – Berkley

Lim G, Burton JC (1982) Nodulation of the leguminosae. In: Broughton WJ (ed) Nitrogen fixation Vol 2. Oxford University Press, New York, pp 1–34

Lin G, Ng HH (1977) nodules of some tropical legumes in Singapore. Plant and Soil 46:317–327

Martin MP (1948) Observations on the nodulation of leguminous plants in the southwest. Plant Study Ser. 4, Regional Bull. 107, Region 6, United States Department of Agriculture, Soil Conservation Service

Martin WC, Hutchins CR (1980) A flora of New Mexico. Ganter, FRG

Meijer EGM (1982) Development of leguminous root modules. In: Broughton WJ (ed) Nitrogen fixation, Vol 2. Oxford University Press, New York, pp 311–331

Nilsen ET, Rundel PW, Shariffi MR (1981) Summer water relations of the desert phreatophyte Prosopis glandulosa in the Sonoran Desert of southern California. Oecologia 50:271–276

Parker HW (ed) (1982) Proc mesquite utilization symposium. College of Agricultural Sciences, Texas Tech University, Lubbock

Parker KW, Martin SG (1952) The mesquite problem of southern Arizona range. United States Department of Agriculture Circular 968. p 70

Pate JS (1976) Physiology of the reaction of nodulated legumes to environment. In: Nutman PS (ed) Symbiotic nitrogen fixation in plants. Cambridge University Press, Cambridge

Quinn MA, Hower AA (1986) Effects of root nodules and taproots on survival and abundance of Sitona hispidulus (Coleoptera: Curculionidae) on Medicago sativa. Ecol Entomol 11:391–400

Rockwood LP (1951) Notes on insects associated with Lupinus polyphyllus Lindl. in the Pacific Northwest. Pan-Pacific Entomol 17:149–153

Rundel PW, Nilsen ET, Sharifi MR (1982) Seasonal dynamics of nitrogen cycling for a Prosopis woodland in the Sonoran Desert. Plant Soil 67:343–353

Scifres CJ, Bovey RW, Fisher CE, Hoffman GO, Lewis RD (1973) Mesquite: Growth, development, management, economics, control, uses. Texas Agricultural Experiment Station Research Monograph 1. Texas A&M University, College Station. p 84

Secor JB, Shanash S, Smeal D, Gennaro AL (1983) Soil characteristics of two desert plant community types that occur in the Los Medanos area of southeastern New Mexico. Soil Science 136:133–144

Sharma E, Ambasht RS (1986) Root nodule age-class transition, production and decomposition in an age sequence of Alnus nepalensis plantation stands in the eastern Himalayas. J of Appl Ecol 23:689–701

Shearer G, Kohl DH, Virginia RA, Bryan BA, Skeeters JL, Nilson ET, Sharifi MR, Rundel PW (1983) Estimates of N_2-fixation from variations in the natural abundance of ^{15}N in Sonoran Desert ecosystems. Oecologia 56:365–373

Shoushtari NH, Pepper IL (1985) Mesquite rhizobia isolated from the Sonoran Desert: physiology and effectiveness. Soil Biol Biochem 17:797–802

Simpson BB (1977) Mesquite – Its biology in two desert scrub ecosystems. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania

Soil Conservation Service (1987) Texas brush inventory. United States Dept of Agriculture, Washington DC

Soltes EJ (ed) (1977) Proc mesquite utilization conference. Department of Forest Science Research Note 4, Texas A&M University, College Station

Sparrow Jr. SD, Ham GE (1983) Nodulation, N_2 fixation, and seed yield of navy beans as influenced by inoculant rate and inoculant carrier. Agronomy J 75:20–24

Tiedeman AT, Klemmedson JO (1973) Effects of mesquite on the physical and chemical properties of the soil. J Range Manage 26:27–29

Vines RA (1976) Trees, shrubs and woody vines of the Southwest. Univ Texas Press, Austin

Virginia RA, Jarrell MW (1983) Soil properties in a mesquite-dominated Sonoran Desert ecosystem. Soil Sci Soc Am J 47:138–144

Virginia RA, Baird IM, La Favre JS, Jarell WM, Bryan BA, Shearer G (1984) Nitrogen fixation efficiency, natural ^{15}N abundance and morphology of mesquite (*Prosopis glandulosa*) root nodules. Plant Soil 79:273–284

Virginia RA, Jenkins MB, Jarrell WM (1986) Depth of root symbiont occurrence in soil. Biol Fertil Soils 2:127–130

Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Matson PA (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238:802–804

Weber CR (1966) Nodulating and nonnodulating soybean isolines. II. Response to applied nitrogen and modified soil conditions. Agronomy J 58:46–49

Weil RR, Ohlrogge AJ (1975) Seasonal development of, and the effect of inter-plant competition on soybean nodules. Agronomy J 67:487–490

Weiser GC, Grafton KF, Berryhill DL (1985) Nodulation of dry beans by commercial and indigenous strains of *Rhizobium phaseoli*. Agronomy J 77:856–859

Wheeler CT, Helgerson OT, Perry DA, Gordon JC (1987) Nitrogen fixation and biomass accumulation in plant communities dominated by *Cytisus scoparius* L. in Oregon and Scotland. J Appl Ecol 24:231–237

Whitson RE, Scifres CJ (1980) Economic comparisons of alternatives for improving honey mesquite-infested rangeland. Texas Agricultural Experiment Station Bull 1307. Texas A&M University, College Station. p 185

Wilson JK (1939) Leguminous plants and their associated organisms. Cornell University Agricultural Experiment Station Memo 221

Woodmansee WG (1978) Additions and losses of nitrogen in grassland ecosystems. BioScience 28:448–453

Wooten EO (1908) The range problem in New Mexico. New Mexico Agricultural Experiment Station Bull 66. New Mexico State University, Las Cruces

Wright RA, Honea JA (1986) Aspects of desertification in southern New Mexico, USA: Soil properties of a mesquite duneland and a former grassland. J Arid Environm 11:139–145